



Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests[☆]

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ABSTRACT

Carbohydrates play a central role in plant functioning because they are building blocks and energy carriers for plant metabolic processes. Because plants are sessile organisms and cannot escape stressful environments they acclimate to unfavourable conditions by strategically allocating carbohydrate resources to overcome stress and promote survival, and build reserves for later use when demand is greater than supply from photosynthesis, like after defoliation. A mechanistic understanding of how plants and, in particular, long-lived organisms like trees allocate and remobilize stored carbohydrates is still very poor. Without such an understanding, however, integration of carbon dynamics from trees to ecosystems and to the globe becomes highly uncertain, especially under ongoing climate change.

Studies of carbohydrate dynamics in trees are often carried out on tree seedlings due to logistical and technical constraints and criticism has been raised whether results can be extrapolated to mature trees. Here we combine a literature review with a critical evaluation of using seedling studies on carbohydrate dynamics to infer mature tree responses that can subsequently be integrated at ecosystem level and beyond. Despite obvious differences between seedlings and mature trees with respect to carbohydrate dynamics, we propose that a combination of approaches, including seedling studies in controlled environments, measurements on mature trees in the field and ecosystem flux measurements, may provide sound estimates of carbohydrate dynamics at larger scales. We show how sensitive predictions of vegetation responses to disturbance are to changes in available reserves and argue that the implementation of more realistic representations of storage dynamics will likely improve simulations of vegetation responses to environmental stress.

1. Carbon allocation in plants: sources, sinks and priorities

Plants are like small factories. Carbohydrates produced during photosynthesis serve as building blocks and energy carriers for the construction of plant biomass. Carbohydrates are partitioned among different sinks and metabolic uses, like growth, life-maintaining functions (respiration, tissue repair/replacement, detoxification etc.), reproduction or storage (Chapin et al., 1990), or can be emitted as volatile organic compounds for communication and defence (Peñuelas and Llusà, 2004) and exported to symbionts or ecological partners like mycorrhiza, rhizobia or soil microbes (Bais et al., 2006; Smith, 1997; Smith and Smith, 2011; Van Rhijn and Vanderleyden, 1995). Sugars and other low-molecular non-structural carbohydrates (NSC) play a

central role in plant functioning not only because they are the substrates for synthesis of other compounds and energy sources for metabolic activities, but also because carbon (C) allocation is mediated by these mobile carbohydrates. Plants also form reserves, i.e. temporarily immobile forms of carbohydrates like starch or C-rich compounds like lipids (e.g., Höll, 1997), and these reserves can be mobilized and re-allocated to metabolic processes when photosynthetic gains are smaller than metabolic demand.

Unlike many other plant life forms, trees can live for centuries or even millennia and over these large temporal horizons the risk of experiencing unfavourable conditions (e.g., herbivore attack, drought) that cause reduced carbohydrate supply is very high (Hartmann and Trumbore, 2016). Carbohydrate storage is thus very important for tree

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survival and fitness, but our mechanistic understanding of how trees allocate and remobilize their resources, in particular stored C, is still very poor and limits our ability to realistically predict tree and ecosystem responses to environmental change (Dietze et al., 2014).

Carbon allocation generally appears to be a very intuitive process in plants. During early seedling development, for example, the radicle emerges in search for water, which is required for the expansion of the hypocotyl and cotyledons to be exposed to light. As the C reserve pool stored in the endosperm slowly depletes, the seed-leaves become the primary source of carbohydrates via photosynthesis. Both the above- and below-ground parts of plants are in what could be described as a functional equilibrium, where the amount of absorptive roots, acquiring nutrients and water, are in balance with the shoot and its associated leaf area providing carbohydrates and other metabolites for both the maintenance and growth of shoot and roots. Thus allocation of carbohydrates among plant organs appears to be a self-regulating process of relocation of resources – from sources to sinks (Gifford and Evans, 1981).

The allocation of carbohydrates among tree organs has been investigated for many decades (Kozłowski and Keller, 1966) and has given rise to hundreds of studies (Lacointe, 2000). C allocation comprises a highly complex set of interacting processes that are driven by organismic nutrient requirements and controlled by physiological, biogeochemical, and ecological constraints. Plants are sessile organisms that cannot escape stressful environments, so they must acclimate to challenging conditions by strategically allocating resources to overcome stress and promote survival. Stress may be imposed by abiotic factors (e.g., moisture and nutrient availability, temperature, and soil chemistry) or by biotic agents such as competition, herbivory, or diseases. Further the allocation of carbohydrates within a plant may be influenced by symbionts like mycorrhiza (Zhang et al., 2015), but also by environmental conditions that limit plant functions, like cold soils that limit root growth and resource uptake (Alvarez-Uribe and Körner, 2007).

Changes in the pool size of different sinks in response to environmental cues can be measured as the change of mass of organs and reserves or as a net change in pool size over time to compute fluxes between pools (Poorter et al., 2012). C allocation may also refer to the distribution of carbohydrates between these pools/sinks in terms of their location (e.g., partitioning among leaves, stems, roots) or their function (e.g., the production of primary and secondary metabolites). Whole-tree carbon allocation studies in mature trees are rare and usually consider only a few components of the tree C balance (e.g., Andersen et al., 2010; Keel et al., 2006). Studies on mature trees comprising several components at the same time are very rare (but see Klein and Hoch, 2015) and usually rely on many assumptions and parameters from other studies. Due to the difficulty in studying mature trees, detailed flux investigations on seedlings and saplings are more common (e.g., Hartmann et al., 2015; Pumpanen et al., 2009), yet it remains uncertain how applicable results from these studies are to the responses of mature trees.

Allocation of carbohydrates in plants is thought to be controlled by the interplay of C sources and potentially competing sinks within in the plant. In general, allocation of C to a given sink may be limited by (1) the source strength, i.e. C supply from photosynthesis and/or remobilization of storage; (2) the rate of translocation of that C via the phloem; (3) the sink strength, i.e. the potential maximum C import rate of a sink when supply is not limiting (Wareing and Patrick, 1975), and (4) sink priority, i.e. “the preferential supply of available photosynthate between competing sinks” (p. 776, Minchin and Lacointe, 2005). When translocation is not limiting, the rate of C allocated to a sink will either be: (1) equal to its sink strength when sink < source strength (i.e. sink limitation) or (2) a function of source strength and sink priority when source < sink strength (i.e. source limitation), with lowest priority sinks being affected most by changes in C availability (Lacointe, 2000). Maintenance respiration is often assumed to have the highest priority,

followed by growth of the canopy and fruit development, then stem cambium and finally root growth (Minchin and Lacointe, 2005). By contrast, storage is often considered to be the lowest priority, with accumulation occurring only when other sinks are C saturated (Dickson, 1989; Minchin and Lacointe, 2005; Minchin and Thorpe, 1987). The physiological mechanisms by which sink priority is manifested are not well understood. Minchin et al. (1993) suggested that the relative position of sinks and sources along the transport pathway could determine hierarchy, with sinks closer to sources having higher priority. Alternatively, genetically regulated changes in sucrose transporters, cell-wall invertases, or in other proteins that affect phloem loading and unloading in sink tissues could be involved (Lemoine et al., 2013).

2. Tree seedlings are convenient for investigations but they're not small mature trees

Trees are impressive organisms; however, they are difficult to study, especially in investigations on processes that affect the whole organism over longer time periods; their great size (both below and above ground) hampers access to some organs (e.g., canopy, root system) and their long lifespan largely exceeds the life expectancy of the researcher. Hence, the temptation is great to use young trees (i.e. seedlings and saplings), and assume that they respond to environmental cues similar to a mature tree. However, these assumptions can be problematic; for example, past investigations on ozone effects on forest trees demonstrated that extrapolating results from seedlings to large trees led to an overestimation of observed ozone damage (Samuelson and Kelly, 2001).

While specific differences between seedlings and mature trees important for carbohydrate allocation will be discussed in later sections, it is obvious that simple allometric proportions (e.g., stem diameter to tree height) do not scale isometrically with tree size. Instead, allometric proportions are generally governed by laws of elasticity and stress resistance or hydraulic relationships that prevent breakage or allow sufficient water transport as trees grow larger (King, 2011; Ryan et al., 2006). Hence, seedlings are not simply small mature trees but change during maturation and this necessarily requires different allocation patterns. In addition, leaf and branch growth is usually constrained to early spring in most deciduous species whereas juveniles may exhibit continuous growth throughout the season (Kozłowski and Pallardy, 1997). This entails substantial seasonal differences in allocation patterns between seedlings and mature trees. In oak trees, for example, the photosynthetic capacity per unit leaf area increases three-fold during tree maturation (Cavender-Bares and Bazzaz, 2000), and this may be due to greater N content in leaves of mature trees (Mediavilla and Escudero, 2003). In other cases, growth and net assimilation rates may decline during tree maturation (Mencuccini et al., 2005). Hence, changes in allometry, photosynthetic capacity, and growth during maturation suggest that allocation of carbohydrates may be different between seedlings and mature trees and making their usefulness for extrapolation to mature trees questionable.

In models, allocation to growth is commonly attributed a higher priority than storage, and hence allocation to storage will largely be determined by the imbalance between source strength (net assimilation) and the sink strength of growth processes. However, the ratio of source to sink strength of growth may shift with tree development: For example it has been shown that the ratio of photosynthetic leaf mass (source) to total living biomass (source + sink) strongly declines with tree size (Poorter et al., 2012) and the ratio of heterotrophic (sink) to autotrophic (source) tissues increases with tree size (Ryan et al., 1995). By contrast, source:sink ratios may increase in field-grown trees with age when soil nutrient availability declines with stand maturation (Binkley et al., 1995; Frazer et al., 1990; Vitousek et al., 1989) and progressively reduces growth sink strength, as documented by slowly attenuating growth rates in elevated-CO₂ field trails on mature or taller trees (Ellsworth et al., 2017; Körner et al., 2005; Norby et al., 2010;

Oren et al., 2001). Declining sink strength in larger trees would therefore lead potentially to a greater accumulation of carbohydrates not used for growth (Körner et al., 2005) than expected from seedling studies. In such investigations, sink strength may be reduced due to lower root growth rates of potted seedlings (where the pots restrict root growth), leading to a higher source:sink ratio and greater leaf starch concentrations than in mature trees (Baber et al., 2014). In tall trees the greater path length of water transport and effects of gravity can lead to greater water stress in the canopies (Koch et al., 2004). Increasing water stress may limit canopy sink strength (Koch et al., 2004; Ryan et al., 2006; Woodruff et al., 2004) and cause NSC concentrations to increase with tree height in canopy tissues (Woodruff and Meinzer, 2011). Considering such differences, direct scaling of C allocation from seedlings to mature trees is questionable.

Despite continuous research activity on C allocation in plants and terrestrial ecosystems during the last decades (Atkin, 2015) our notoriously vague understanding of the underlying control mechanisms makes modelling of C allocation in trees a major challenge (Franklin et al., 2012). Studies that addressed molecular controls of carbohydrate allocation in leaves to provide mechanistic relationships for modelling are limited to biannual herbs and cover diel dynamics only (Smith and Stitt, 2007), so their relevance for long-lived organisms like trees is uncertain (Hartmann and Trumbore, 2016). Because the effects of changes in C allocation in response to environmental stimuli, like rising temperature, increasing atmospheric $[\text{CO}_2]$, or altered precipitation, extend from physiological processes to regional and even global energy and element fluxes (Anderegg et al., 2013; Keenan et al., 2014) modelling becomes an essential tool in predicting such fluxes at broad spatial and temporal scales. A quantitative understanding of how plants allocate C resources is needed for realistically forecasting vegetation responses to future environmental conditions (Mooney, 1972), but upscaling of C allocation processes conveniently measured in seedlings or more challengingly obtained from mature trees to whole ecosystems and beyond implies high uncertainties (Sitch et al., 2008).

This opinion paper combines a literature review with a critical evaluation of the usefulness of seedlings studies on C allocation (and, more specifically, on carbohydrate reserve dynamics) for inferences on mature trees and for simulating vegetation responses to environmental cues. We first review the dynamics of non-structural carbohydrates concentrations across spatial and temporal scales in tree tissues. We also focus on the regulation of carbohydrate storage and remobilization and how environmental stress influences tree carbohydrate concentrations. We then present how C allocation, in particular to storage, is currently represented in vegetation models and how sensitive predictions of vegetation responses to disturbance are to changes in available reserves. Finally, we indicate how manipulations of seedlings under controlled environmental conditions can be combined with field observations and manipulations of mature trees to allow further insights into tree C dynamics that can improve implementations of C allocation in vegetation models.

3. Spatial and temporal distribution of carbohydrates within trees

3.1. Carbon storage pools in trees

In mature trees, the largest fraction of non-structural C reserves is often stored in stems and roots, mainly as starch, but also as storage lipids (triglycerides) in numerous tree species (Hoch et al., 2003). In wood, storage is restricted to the living cells of the radial and axial parenchyma of the sapwood. Accordingly, there is a close correlation between the fraction of parenchyma and the concentrations of C reserve compounds in the wood of tree stems and roots (Plavcova et al., 2016). Concentrations of C storage compounds are often significantly lower in stem and root wood tissue than in the associated phloem (i.e. bulk of conducting and non-conducting secondary phloem), leaves, and young branches, but due to the large biomass of wood in stems and coarse

roots, these organs are quantitatively the main storage pools in most mature trees, especially in broadleaved trees (Barbaroux et al., 2003; Würth et al., 2005). In evergreen tree species, especially in the conifers of temperate and boreal climates, mature foliage, and in some species also bark and phloem tissues, can further store an important portion of C reserves (e.g., Hoch et al., 2002; Ludovici et al., 2002).

Seedlings and saplings differ significantly from mature trees in terms of C-storage compartmentalization. The most obvious difference is the lack of a large stem and structural roots and the absence of non-storing heartwood and older sapwood. Carbohydrate reserve concentrations of the small stems of tree seedlings are often higher than those found in mature tree stems, but are similar to those in found in young branches of crowns in mature tree. For example, using the same method for NSC analyses, Weber et al. (2018) found about three to four times higher NSC concentrations in the sapwood of stems in 2-year old seedlings than have been reported for the sapwood of 100 year old trees of the same species (Hoch et al., 2003). The same goes for roots of seedlings, where C reserve concentrations resemble that of smaller roots in mature trees of the same species. In aspen, for example, NSC concentrations in roots of seedlings are about two times higher compared to mature trees (Galvez et al., 2013; Landhäusser and Loeffers, 2003).

During ontogeny, trees undergo significant changes in the biomass ratios of their individual organs, which in turn will have a significant impact on the carbohydrate reserve allocation dynamics and storage pools. These changes can differ among species, but some patterns are more general. For example, trees show a marked decrease of their root to shoot ratio (e.g., Genet et al., 2010; Vanninen et al., 1996), and their leaf to wood ratio (e.g., Poorter et al., 2015) with age. Seedlings and small saplings typically also exhibit higher proportions of bark (phloem) in relation to their total biomass than adult trees. Hence, although the total C reserve pool of trees increases with tree size, it does not scale linearly as proportions of older and non-storing tissues increase with tree age. This will result in lower bulk concentrations (i.e. the biomass weighted mean concentrations across all tree organs) of C reserves in mature trees compared to seedlings and saplings.

3.2. Seasonal carbohydrate storage dynamics in mature and young trees

Carbohydrate reserves are used in tree tissues whenever the current supply of photosynthate does not satisfy the C demand for growth, respiration and other plant functions. In seasonal climates, reserves are consumed for new growth immediately after bud break, but they recover quite quickly particularly in tissues close to the source (i.e. leaves, Landhäusser, 2011; Schädel et al., 2009). In evergreen conifers of temperate forests, C reserves are built up immediately before bud break in needles and young branches and decline subsequently throughout the season in these organs (Hoch et al., 2003). The loss of C reserves during winter is low in temperate and boreal ecosystems (Landhäusser and Loeffers, 2003; Wieser, 1997), but can be substantial in ecosystems, such as Mediterranean regions, where the dormant period occurs during dry hot periods (Palacio et al., 2007). Changes in tissue concentrations of C reserves (showing the remobilization of stored C) vary among organs and are usually small across the season in the stems of mature trees, while more substantial in the youngest branches and fine roots (e.g., Hoch et al., 2003; Klein et al., 2016; Landhäusser and Loeffers, 2003).

A meta-analysis of 121 studies covering 177 species showed that the seasonal changes of C reserves are moderate in mature trees, indicating that a substantial fraction of the stored C is not used under 'normal' conditions (Martínez-Vilalta et al., 2016), but might be re-mobilized for recovery and re-growth after environmental stress or disturbance (Carbone et al., 2013). Starch shows greater seasonal concentration changes than low-molecular-weight sugars, indicating the exclusive reserve function of the former, and the multi-functional nature of the latter compound class (Martínez-Vilalta et al., 2016).

Seasonal C-dynamics of trees are basically driven by phenology, i.e.

the beginning of leaf flush and wood growth, the timing and amount of seed production, as well as the end of wood formation and leaf senescence (Martínez-Vilalta et al., 2016). In deciduous tree species of temperate biomes, there is a stark difference in the start of the spring leaf flush between young, sub-canopy and mature trees which generally flush later than their conspecific saplings in the understory (Augspurger and Bartlett, 2003). This difference in the timing of bud break can be up to several weeks, and it is likely driven by ontogenetic changes, rather than the climatic differences between canopy and understory (Vitasse, 2013). By contrast, bud set and leaf senescence often occur earlier in the season in mature trees than in saplings and seedlings (Hoch, G. pers. observation, Augspurger and Bartlett, 2003; Gressler et al., 2015). Earlier leaf flushing and later leaf senescence enables seedlings and saplings to profit from better light conditions for photoassimilation very early and late in the season. This leads to an overall longer growing season in young trees with consequently potentially different seasonal dynamics of C reserve compounds, and net seasonal C-balances in seedlings compared to mature trees. In addition, a low-light understory might induce a preferential allocation of C to storage in young shade tolerant sub-canopy trees in order to better survive the deep-shade conditions during most of the season (Kobe, 1997).

3.3. Carbon reserves and reproduction in trees

One major difference between young and mature trees is allocation to reproduction. The formation of fruits and seeds constitutes a C demand that could alter C reserve dynamics in mature trees relative to seedlings. Within a given tree species, the magnitude of this sink can vary significantly among years, depending on climatic conditions. Many tree species show also a distinct masting behavior, where a season with substantial reproduction alternates with one or several years with less or no reproduction (Kelly, 1994; Koenig and Knops, 2005). While there are still many unanswered questions about the biological mechanisms behind masting and variable seed production in perennial plants in general (Miyazaki, 2013; Moreira et al., 2015; Pearse et al., 2014), substantial progress has been made over the last years in describing the role of C reserves for reproduction, as well as the influence of reproduction on the C balance of trees. Against previous assumptions, even mast seeding might not directly use stored C reserves in mature trees. Instead, there are experimental and observational data suggesting that the C supply for regular reproduction is exclusively from current year photoassimilation, as many seed producing structures in trees such as flowers parts, fruits and cones are photosynthetically active (Hoch et al., 2013; Ichie et al., 2013). However, the higher C demand for seed and fruit production within the canopy during a high reproduction year might limit the C supply for other sinks like cambial growth, resulting in lower wood production during masting years (Hackett-Pain et al., 2015; Mund et al., 2010; Selås et al., 2002), especially in tree species which infructescences are largely photosynthetically inactive (i.e. the woody cupulae of beech species).

3.4. Section summary

The differences in seasonal carbohydrate reserve dynamics between young and mature trees can be significant and are largely driven by differences in the relative ratios of different tissues and organs, and by differences in phenology. The amplitude of seasonal changes in C reserves is more pronounced in tree seedlings and young saplings, resembling more closely those of young branches and small roots in mature trees. Hence studies on tree seedlings can deliver general information on the seasonal dynamics of C source-sink-relations in trees, but they should be used with caution whenever reserve pools are scaled quantitatively from seedlings to mature trees.

4. Storage and remobilization processes and their regulation

4.1. Is storage a competing sink?

One of the big, unanswered questions regarding the regulation of storage is to what degree storage competes for C with other sinks such as growth (Dietze et al., 2014). Typically, NSC storage is considered the lowest priority sink (Dickson, 1989; Minchin and Thorpe, 1996; Minchin and Lacomte, 2005), in which case, net storage would only occur when other sinks are saturated or transport to these sinks is inhibited. Recent debates on the mechanisms of drought-induced tree mortality have highlighted that storage is not merely a process of accumulation when supply exceeds demands, but a highly regulated process (Sala et al., 2012) that results in part from reserve formation at the expense of growth (Chapin et al., 1990) as a means to promote future survival in long-lived organisms (Wiley and Helliker, 2012). In seedlings, greater storage can increase the chance of survival under low light or following canopy disturbance (Canham et al., 1999; Myers and Kitajima, 2007), underscoring the assumed tradeoff between growth and low-light survival in shade tolerant versus intolerant species (Kobe, 1997; Myers and Kitajima, 2007). However, this may not occur in mature canopy trees, which are less likely to experience low light conditions. Still, there is evidence suggesting that storage can compete with growth in larger trees as well. For example, rubber tapping decreases growth but increases wood NSC concentrations (Chantuma et al., 2009) and branch shading reduces growth but not NSC concentrations (Lacomte et al., 2004). In these cases, net storage occurs even though growth is apparently limited by C availability. The degree to which storage competes with growth, how the priority of storage may change under different conditions, and how seedlings and mature trees may differ in these regards remain large unknowns.

4.2. Remobilization of stored NSC

The remobilization of NSC storage pools contributes to the C supply for respiration, growth and other functions. Therefore accurate modelling of C allocation requires knowledge about how much and when stored C is remobilized. Unfortunately, the factors regulating both storage and remobilization remain very poorly understood in trees. Additionally, we do not know how much of the existing storage C is available for remobilization. While analyses of nuclear-bomb-spike radiocarbon (Trumbore, 2006) have shown that C remobilized in mature trees following severe disturbance can be several years to several decades old (Carbone et al., 2013; Muhr et al., 2013; Muhr et al., 2016), a portion of NSC, including starch, may be permanently sequestered in mature trees (Millard et al., 2007). Also, not all sugars function as storage molecules; instead a portion may be seen as a plant's cash flow (Klein and Hoch, 2015), act—particularly in tall trees—as osmoregulators to cope with the negative effects of height on water potential (Sala et al., 2012) or may be used for synthesis of secondary metabolites (Gershenzon, 1994). Other compounds like proteins and lipids are rarely assessed in allocation studies, though they can serve as energy sources when carbohydrates become depleted (Fischer et al., 2015).

Inferences about remobilization in mature trees from seedling studies may be problematic if the proportion of the NSC pool not functioning as storage (e.g., osmolytes; Sala et al., 2012) differs; which this is fully unknown. Further, of the NSC that is available, it is unclear whether the degree of remobilization is controlled by sink strength (e.g., if early leaf growth is limited by N not C; Cheng and Fuchigami, 2002) or by the amount of reserves (i.e. source strength). And while NSC storage pools show similar proportions of seasonal depletion in mature trees (30–50% unremobilized in stemwood and/or roots Hoch et al., 2003; Martínez-Vilalta et al., 2016) and seedlings (> 33% unremobilized in perennial tissues in walnut 30% following budbreak, Lacomte et al., 1993), potential differences in the degree to which

remobilization in seedlings and trees may be sink or source limited have not been explored yet.

Finally, while it is generally assumed that storage pools are not usually mobilized during times of peak photosynthetic gain (i.e. during the growing season) or in the absence of stress, it has been shown that stored C partly fuels stem respiration during early summer for beech and during early and late summer in spruce (Kuptz et al., 2011). In addition, C emitted from stem respiration during the growing season can be up to 6 years old, and even older deeper within the stem (Mühr et al., 2013; Trumbore et al., 2015). These results suggest that stored C is constantly being remobilized to support metabolism, even during times when C supply is greater than demand. Inferences from manipulations of small trees on reserve dynamics in mature trees may underestimate the use of old reserve pools.

4.3. One pool fits all?

NSC storage is often modelled as a single pool, however NSC are distributed throughout the plant in different organs with varying distances from major carbohydrate sinks, like apical or secondary meristems. The spatial arrangement of these pools may lead to different patterns of storage and remobilization with little integration, making it problematic to treat the storage pool as a single entity (Hartmann and Trumbore, 2016). Instead, storage should perhaps be considered as multiple C pools that may be regulated independently and have different turnover times (Keel et al., 2007). For example, different organs can have contrasting NSC concentration dynamics in both mature trees (Gregory and Wargo, 1986; Landhäusser and Lieffers, 2012; Saffell et al., 2014) and seedlings (Lacointe et al., 1993). Also, *within* an organ, remobilization has been hypothesized to follow the rule of “last in, first out” (Lacointe et al., 1993) where younger C (< 1 year old) is preferentially used for root growth (Lynch et al., 2013; Vargas et al., 2009) and for stem growth and respiration in mature trees (Carbone et al., 2013), but after major disturbances, older C is used to fuel regrowth (> 10 years old; Carbone et al., 2013; Vargas et al., 2009). Similarly, in 3-year old walnut seedlings, starch formed in October is remobilized earlier and to a greater extent in the following growing season than older starch formed in August (Lacointe et al., 1993). This suggests that the youngest reserves are deposited in the youngest cells, which are closer to the phloem and cambium tissues and are first to be mobilized (Earles et al., in press).

4.4. Sections summary

Much remains unknown about the processes controlling storage and remobilization of NSC, in both seedlings and mature trees. How much NSC and which pools (in different organs, different compounds) are available for remobilization is largely unknown and may be different in seedlings and mature trees, due to differences in size and tissue age. Seasonal remobilization dynamics are similar in seedlings and mature trees, but inferences on the use of older reserves from studies on seedlings can only be made when old is defined relative to tree age. Similarly, storage pool turnover times, also proportional to tree age, can be assessed in seedlings but further studies, ideally using isotopic labelling of storage inputs (Hartmann and Trumbore, 2016), are required to clearly show whether trees in general, and seedlings in particular, have more than a single C storage pool.

5. Carbohydrates in trees during environmental stress and resource limitation – a matter of source or sink limitation?

5.1. The influence of environmental stress that can directly affect growth and photosynthesis on source-sink relationships

Increasing duration of environmental stress, such as from temperature extremes and drought, can reduce rates of growth and

photosynthesis, affecting both C acquisition and allocation (Adams and Kolb, 2004; Lambers et al., 2008). However, growth is often much more sensitive than photosynthesis to temperature and drought stress (Pisek and Winkler, 1959). Under low temperature, cell growth approaches zero near 1–2 °C in cold-adapted plants (Körner, 1998), yet photosynthesis of trees is only reduced to 30% of maximum (Körner, 2003; Körner, 2015; Tranquillini, 1979). For drought, the difference between levels of water stress that limit growth and those which completely close stomata can be fairly large, and photosynthetic rates are only slightly reduced when growth ceases in a variety of species (Muller et al., 2011 and references therein). Although the dominance of sink limitation over source limitation during drought and low temperature stress is gaining traction in plant physiology (Körner, 2015; Kozłowski and Pallardy, 1997; Lambers et al., 2008), differences in the dominance of sink and source limitation between trees and seedlings are poorly studied.

Research on the response of NSC reserves in trees and seedlings to abiotic stresses (e.g., temperature, drought) can provide insights into variation of NSC stress responses with tree size and ontogeny. NSC responses to cold and non-lethal drought are generally similar and increases are observed more often than decreases and many investigations have shown NSC increases in seedlings and mature trees at low temperature (Bansal and Germino, 2008; Bansal and Germino, 2010; Fajardo et al., 2011; Fajardo et al., 2013; Hoch, 2015; Hoch and Körner, 2003; Hoch and Körner, 2012; Piper et al., 2006; Shi et al., 2008), consistent with sink limitation. Drought effects on NSC reserves can be separated into two groups: experiments and observations of drought that were lethal and non-lethal, e.g. those where seedlings or trees survived drought. Non-lethal drought reduced growth and increased C allocation to NSC reserves consistent with sink limitation in mature tropical shrubs (Tissue and Wright, 1995), temperate mature pines (Gruber et al., 2012; Piper et al., 2017; Sala and Hoch, 2009) and mature Mediterranean angiosperms (Körner, 2003). Fewer studies report reduced NSC consistent with source limitation under non-lethal drought (but see Rosas et al., 2013) but it has been shown for mature trees, in leaves of several Mediterranean shrubs and trees (Körner, 2003), roots of subtropical (Sayer and Haywood, 2006) and Mediterranean pines (Klein et al., 2014), and stems of semiarid pines (Adams et al., 2015). For seedlings under non-lethal drought stress, little data supports source limitation (but see Maguire and Kobe, 2015) and even increases in NSC reserves have been documented (Bachofen et al., 2018; Galvez et al., 2011).

The effect of lethal drought, defined as drought stress resulting in whole-plant death, on carbohydrate allocation in seedlings, saplings, and trees appears highly variable among species. A synthesis of lethal drought stress studies found that sapling, seedling, and mature tree NSC near death from drought was lower in plants that died than for survivors or watered controls in only about half of the cases (48% of cases and 38% of species) for at least one organ (Adams et al., 2017; Dickman et al., 2015; Sevanto et al., 2014). NSC responses to lethal drought did not appear to depend on ontogeny, as seedlings, saplings and mature trees each had divergent responses among studies, but overall, gymnosperms were more likely to show reduced NSC at death than angiosperms (Adams et al., 2017). Despite decades of research on temperature and drought stress effects on NSC in seedlings, saplings, and mature trees of multiple species from different biomes, no consistent differences in source-sink responses between ontogenetic life stages have emerged.

5.2. The influence of environmental factors that directly limit photosynthesis, but not growth, on C allocation

Research on the effect of tree size and life stage on carbohydrate allocation in response to environmental factors that directly limit C uptake, but do not directly limit allocation to growth, is also lacking in the literature. However, factors such as reduced light availability and

low CO₂ concentrations that reduce photosynthesis without directly limiting C allocation to growth have consistently resulted in NSC reductions. Reduced NSCs in total darkness have been observed in small mature trees of *Pinus edulis* (Sevanto et al., 2014) and in seedlings of *Pinus nigra* (Fischer et al., 2015), *Acer pseudoplatanus* (Piper and Fajardo, 2016), *Populus tremuloides* (Wiley et al., 2017) *Quercus petraea*, *Acer pseudoplatanus*, *Picea abies* and *Pinus sylvestris* (Weber et al., 2018), as well as in ten tropical tree species (O'Brien et al., 2014). Data from low light and low CO₂ experiments are mostly limited to potted seedlings and saplings, but in one field study on mature *Pinus contorta*, shading reduced NSC after one growing season (Fraser et al., 2006). Reductions in NSC reserves after low light treatment, but prior to drought, have been predictive of time to death from drought in seedlings, suggesting that NSCs play a crucial role in surviving source limitation (Myers and Kitajima, 2007; O'Brien et al., 2014). Several experiments that combine low light or low CO₂ treatments with lethal drought have found that these source-limitation treatments reduce NSC more and/or faster than drought alone in seedlings (Hartmann et al., 2013; Piper and Fajardo, 2016; Quirk et al., 2013), and small (2–2.5 m tall) mature trees (Sevanto et al., 2014). No clear differences emerge among life stages in C allocation responses to limited C uptake, as was seen for environmental stresses that affect both growth and photosynthesis directly (Section 5.1), perhaps because such data are very limited for mature trees.

5.3. A hypothesis for differences in carbohydrate dynamics between seedlings and mature trees

Few studies have examined patterns in source-sink dynamics of carbohydrate allocation across tree life stages within a field site or experiment, limiting our ability to use experiments performed on seedlings and saplings to infer mature tree responses (Machado and Reich, 2006). Here we suggest combining experiments on seedlings with observations (and, where possible, manipulations) on mature trees in the field that allow linking the different scales. We hypothesize that seedlings and mature trees will have similar physiological responses to temperature or drought stress, in that growth will be reduced before photosynthesis, but that because seedlings exploit less environmental space, and have access to smaller pools of water and NSC that can be more rapidly depleted, they should be affected earlier by changes in their source and sink activity than mature trees (Fig. 1). As environmental stress persists, C reserve responses are less certain, and NSC may remain high, increase, or decrease, which may depend on specific environmental stressors, but also their duration and severity. Studies investigating the effects of ontogeny on allocation responses to stress or resource limitation for the same species within the same study, either at the same field site, or using the same experimental treatments can be insightful for elucidating the fate of carbohydrate reserves during prolonged environmental stress. Experimental manipulations that directly limit C uptake without directly affecting C allocation to growth (e.g. low light and/or CO₂), when combined with drought or temperature stresses that do directly affect growth and photosynthesis, can provide insight into source vs. sink dynamics, and also help disentangle effects on sink strength vs. sink priority.

5.4. Section summary

Differences in carbohydrate responses to stress that can directly affect growth and photosynthesis and responses to stress that reduce only photosynthesis without affecting allocation to growth are well-documented in the literature. However, there is no overall support for an effect of ontogeny or plant size on carbohydrate allocation patterns for either type of environmental stress. For all tree life stages, allocation responses to low temperature and drought are predominately consistent with sink limitation, although when drought was severe or persistent enough to be lethal this consistency was reduced. Under C uptake

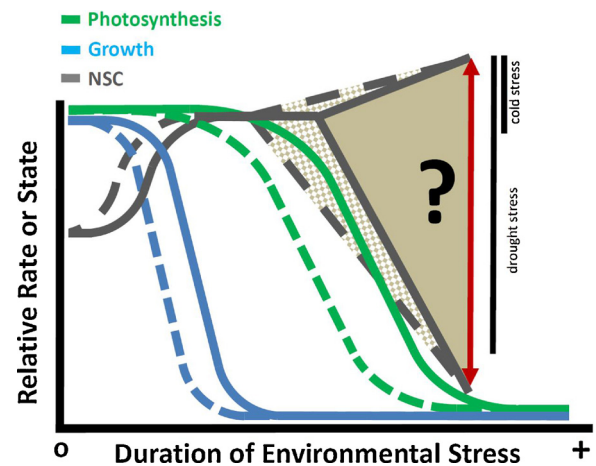


Fig. 1. A hypothesized framework for C dynamics under environmental stress that limits growth and photosynthesis directly (e.g. temperature and drought). Initially, C allocation is not limited in the absence of environmental stress. Under moderate stress, growth is limited before photosynthesis, causing increased C reserve accumulation in non-structural carbohydrates (NSCs) consistent with sink limitation. We hypothesize that seedlings (dashed lines) will have the same functional responses to temperature and drought as mature trees (solid lines), reduced growth prior to reduced photosynthesis, but that these responses will occur earlier for seedlings because they access and exploit less environmental space than mature trees. As environmental stress persists, C reserve responses are less certain (grey area), and NSC may remain high, increase, or decrease, which may depend on specific environmental stressors. The amplitude of the cone (red arrow) may vary between seedlings and mature trees. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

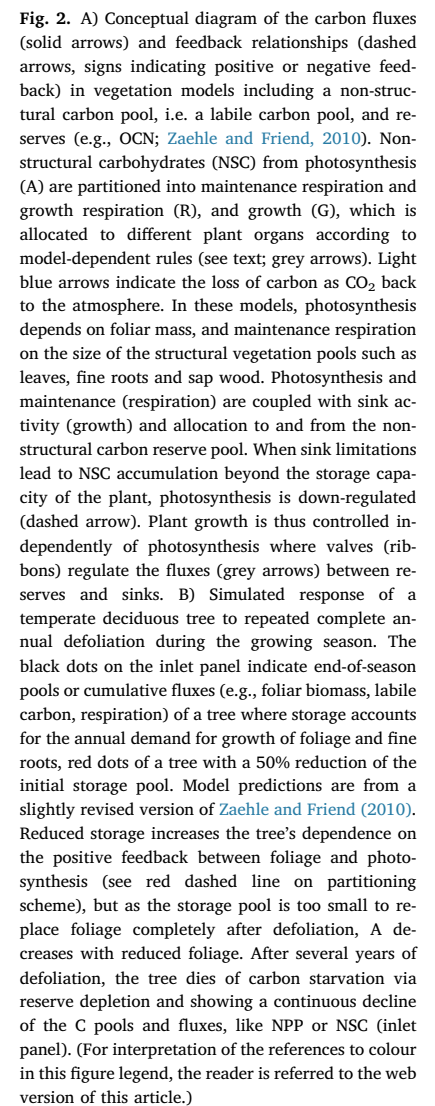
Figure adapted from McDowell, 2011.

limitation via low light or low CO₂, NSC typically declined, but little data for mature trees constrains any assessment of life stage or size effects on this response. This gap in our understanding creates uncertainty but also the opportunity to develop hypotheses that need to be addressed in experimental studies. The resulting information can then be used to predict responses of mature trees and integrated at larger scales (see Section 7).

6. Carbon allocation in vegetation models

Vegetation models integrate (eco-) physiological process understanding to simulate growth and decay of plants for entire ecosystems and at the scale of seasons and beyond. The development of such models has focussed on determining C acquisition by the canopy (Rogers et al., 2017), plant C loss to respiration (Dewar et al., 1999; Thornley and Cannell, 2000), and the representation of community dynamics, scaling processes from individual trees to ecosystems (e.g., Medvigy et al., 2009; Smith et al., 2001). Conversely, the representation of C allocation and storage is – in many ways – the stepchild of vegetation models. Plant growth in vegetation models is commonly simply defined as the difference between instantaneous rates of C acquisition and respiration and its allocation to a number of plant organs, such as leaves, fine roots, and woody tissue (Fig. 2A).

In their simplest form, allocation models assume a fixed partitioning of assimilates to different plant organs (De Kauwe et al., 2014 for an overview; see Franklin et al., 2012). This widely-used approach allows capturing average C allocation patterns observed in global biomass databases (e.g., Litton et al., 2007). A growing number of models represent growth of individual trees or at least cohorts of trees of similar age or size (Medvigy et al., 2009; Smith et al., 2001). These models are in principle able to track changing growth and allometry patterns of a tree from small to mature trees as discussed earlier, including for instance different reproduction strategies at different ages, even though this is often not done. Size enters growth calculations typically through the pipe-model, i.e. assuming a constant ratio of sapwood and leaf area

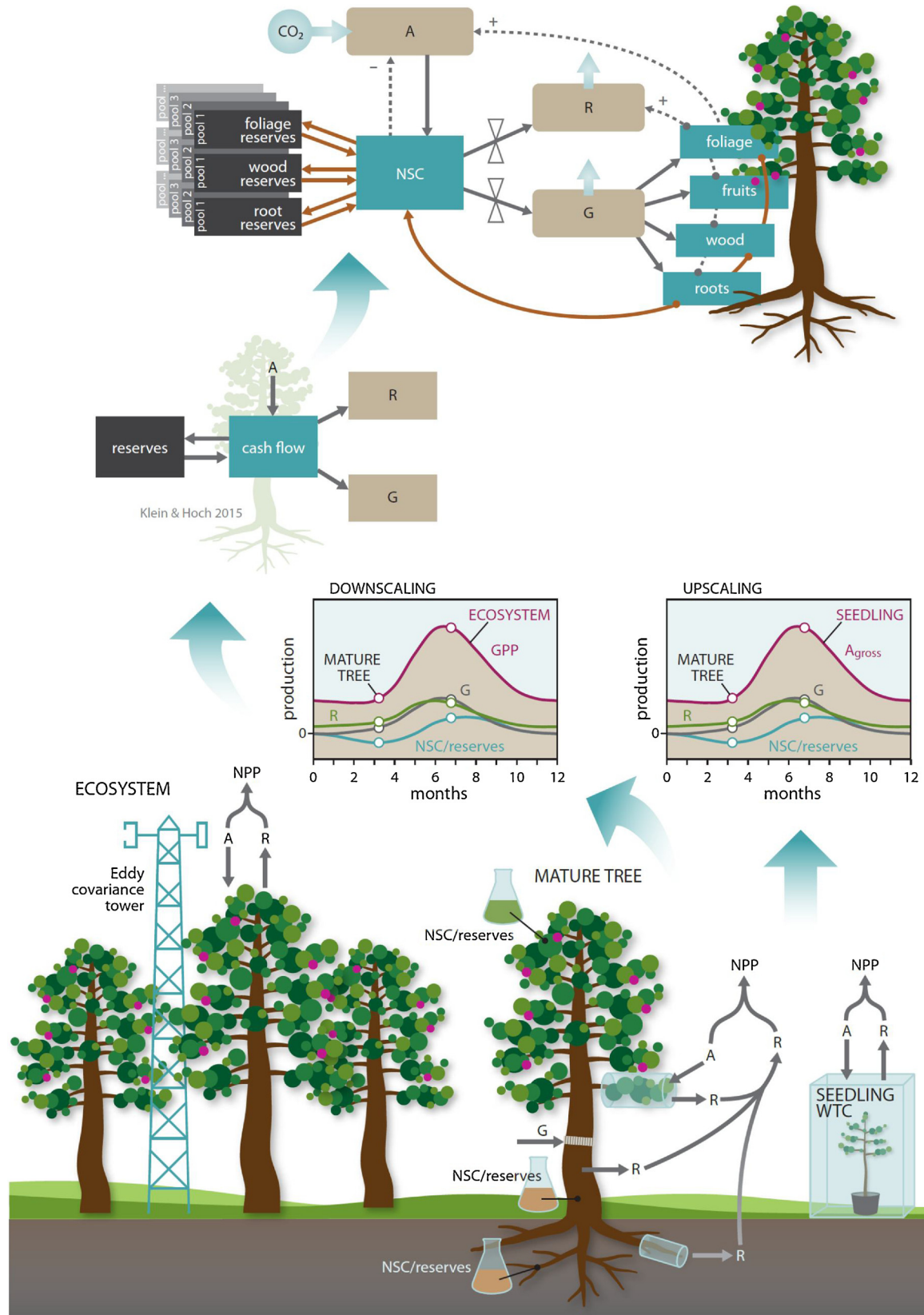


Most allocation models were originally developed to represent growth integrated over timescales of years and longer and therefore lack a representation of seasonal or interannual variation in allocation pattern or storage. However, in recent years, there have been attempts to overcome this limitation by introducing a fast non-structural pool that decouples net C gain from growth and a longer-term storage pool which buffers variability in growth in addition to allowing for the seasonal display of foliage and growth of roots (Ceballos-Núñez *et al.*, 2017; Fisher *et al.*, 2010; Richardson *et al.*, 2012; Zaehle and Friend, 2010). While such an approach appears intuitive, there is uncertainty about: 1) mechanisms and processes that govern non-structural C dynamics. Examples of these are the factors that determine the build-up and use of non-structural C controlled in response to plant-internal (e.g., beginning and ending of the growing season, imbalance between C and nutrient acquisition) or environmental (e.g., temperature, moisture deficit) signals; and 2) the search for an appropriate, yet

How can information obtained from observations and experiments on seedlings and mature trees inform large-scale vegetation models? One promising approach to overcome the scale gap between tissue-level measurements of NSC and the conceptual pool and flux structure of a process-oriented model has been proposed by [Klein and Hoch \(2015\)](#). In their study, a number of different observations (e.g., leaf-level assimilation, growth measurement, stem and root respiration, NSC concentrations in different tree organs, eddy covariance flux measurements) were compiled into a whole-tree C budget (via mass balance) and synthesised in a conceptual model of NSC pool dynamics describing the fluxes between the labile pool “cash flow” and storage. By integrating seasonal and interannual NSC dynamics at ecosystem level, their approach can provide empirically-derived parameters that can easily be mapped onto the structure of process-oriented models (e.g., characteristic turnover times for the labile pool, and exchange coefficients describing the mobilization of the storage).

The potential implications for the appropriate and robust representation of such developments are the ability to account for the sink versus source limitation of growth, as well as the lagged responses to perturbations. Indeed, introducing such short and long-term storage

pool terms can have profound effects on the ability of a model to simulate perturbation responses, as noted by Fisher et al. (2010). Fig. 2B demonstrates that the ability of a simulated tree to recover from repeated defoliation depends on its storage pool size, where trees die



(caption on next page)

Fig. 3. Suggested framework for combining investigations on seedlings with observations (and field manipulations) on mature trees and ecosystem flux measurements (e.g., eddy covariance). Seedling studies, like whole-tree chamber (WTC) measurements, allow continuous and temporally highly resolved assessments of carbon fluxes and pools (e.g., carbon assimilation (A), respiration (R), growth (G), NSC) across entire growing seasons. Such investigations are often not feasible on mature trees in the field. Discrete measurements on mature trees can be matched with seasonal dynamics obtained from seedling, providing estimates of seasonal mature tree dynamics. Furthermore, ecosystem flux measurements provide constraints for integration of mature tree measurements at ecosystem scale, thereby allowing quantitative partitioning into individual flux components (A, R, G, NSC). Such flux partitioning provides an empirical link between measurements on seedlings and mature trees and ecosystem-scale observations (e.g., eddy covariance) and produce parameter estimates for seasonal NSC dynamics (storage vs. cash flow) and allocation to other sinks, like litter or exudation (not shown in figure, Klein and Hoch, 2015). The resulting parameters estimates can inform forest and vegetation models by providing more realistic representations of both NSC reserve formation and mobilization. Ideally, such reserve pools can be defined for different plant organs (foliage, wood [branches and stem], and roots) and by different turnover times (e.g., slow and fast turnover pools, indicated by cascade of pools) or by successively older pools, analogous to tree rings formed by secondary growth.

when storage pools are reduced to 50% of the annual C demand for growth of foliage and fine roots. This illustrates the potential utility of such a modelling framework for providing realistic representations of NSC dynamics and their role for tree growth and survival during environmental stress.

6.1. Section summary

While vegetation models are beginning to represent NSC dynamics, there is a lack of knowledge of how to constrain these models with observations and select an appropriate model structure. Synthesising observations into simple, conceptual, but mathematical explicit frameworks may be an approach to overcome the scale gap between measurements and models. Information from repeated NSC measurements will allow constraining important model functions such as the response of storage pools to environmental cues or stresses.

7. From seedlings and mature trees to ecosystems and beyond

The previous sections have highlighted both similarities (e.g., seasonal NSC dynamics) and differences (e.g., absolute concentration in specific organs) between seedlings and mature trees. Because the regulation of storage and mobilization of reserves is in general still not well understood we can only hypothesize that source activity in seedlings may be affected by stresses earlier and likely more severe than in mature trees, with uncertain consequences for NSC dynamics (Fig. 1). Hence there is no clear answer to the question whether and to what degree inferences on mature trees can be drawn from studies on seedlings. However, because manipulations and observations of mature trees are challenging, studies on seedlings remain important data sources, especially when whole-plant processes like changes in storage allocation in response to stress are considered.

Ongoing environmental change characterized by rising temperatures and more frequent drought episodes (IPCC, 2013) may have substantial impacts on tree physiological processes and tree survival (Allen et al., 2015). Vegetation models are important tools for process integration and for predicting forest responses to environmental change. However, their ability to simulate plant responses to drought and heat are limited (Sitch et al., 2008) and this still prevents realistic predictions of future forest condition (Hartmann et al., 2018). Improving model predictions requires implementation of more realistic NSC dynamics than currently available, where NSC buffer C deficits spanning hours to months, but longer-term dynamics are not well defined (Dietze et al., 2014). The current state of knowledge supports the idea that storage pools can buffer deficits over several growing seasons; for example, the turnover time of mobilized sugars in tree stems of sugar maple is between three to five years (Muhre et al., 2016). An important emphasis of future model development (and experimental data to constrain this) will be to determine the time-scale, the rate and the costs, at which C storage pools can be remobilized. C storage dynamics can be represented in vegetation models by implementing reserve pools with different turnover times or successively increasing age, analogue to tree ring formation from secondary growth (Fig. 3). These reserves should then be available for mobilization and metabolism, in particular under resource limitation or during recovery (Carbone et al.,

2013; Muhre et al., 2013; Vargas et al., 2009). Model formulations that constrain C storage to seasonal or interannual foliage replacement will necessarily underestimate the role of older C reserves for survival and stress responses depicted in Fig. 1 may need to be considered in these implementations.

Seedling studies, like whole-tree chamber (WTC) measurements, allow continuous assessments of carbon fluxes and pools (e.g., assimilation, respiration) across entire growing seasons, which are usually not feasible on mature trees in the field. Where parameters for NSC dynamics of mature trees are lacking, seedling studies can provide best estimates (e.g., seedling stem NSC pools size as estimate for branch NSC in large trees, see Section 3) for mature trees. In other situations data can be collected directly and repeatedly on mature trees (e.g., stem NSC concentrations, stem respiration rates) during the growing season and may be matched with seasonal dynamics from seedlings and constrained by flux measurements at ecosystem scale (e.g., eddy covariance), thereby allowing quantitative partitioning of individual flux components (Fig. 3). This flux partitioning thus provides an empirical link between measurements on seedlings, mature trees and ecosystem-scale observations and can produce parameters of seasonal NSC dynamics for different plant organs (Klein and Hoch, 2015), a promising step toward empirically derived NSC dynamics required for improving realism of forest and vegetation models (Dietze et al., 2014).

More research on carbohydrate storage regulation is needed. Comparisons between modelled vegetation responses and observations in the field allow developing hypotheses for experiments in controlled environments. Some of these experiments will be necessarily on seedlings as manipulations of mature trees in the field are not always feasible, especially when whole-tree processes (e.g., carbon balance) are addressed. In particular, manipulations of source-sink relationships are needed to elucidate control mechanisms of carbohydrate allocation in general and storage regulation in particular. Experiments may use shading, low CO₂, cold temperature or pruning for manipulating source and sink activity and must apply a multitude of methodologies, including isotope pulse-tracer or continuous isotopic labelling as well as atmospheric radiocarbon signals, to advance our process understanding of tree physiology in a changing world (Hartmann and Trumbore, 2016).

Conflicts of interest

None.

Contributions

All authors have contributed equally to (1) the conception and design of the study (not applicable: acquisition of data, or analysis and interpretation of data), (2) drafting the article and revising it critically for important intellectual content. Furthermore (3) all authors have given their final approval of the version to be submitted.

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